In the EEG analysis, the reported source areas of the phase synchrony included the inferior frontal gyrus, anterior cingulate, parahippocampal gyrus, and postcentral gyrus. However, further confirmation of the exact brain regions would be welcome because all linear source estimates of scalp EEG, including standardized low resolution brain electromagnetic tomography (sLORETA) employed by Yun *et al.*, suffer from significant point spread and cross-talk. Therefore, the distance between the source points cannot be equated with spatial resolution, which, instead, is mainly determined by the distance of the electrodes from the sources and the electromagnetic properties of the head. The high statistical significance of the estimate at certain grid points indicates a significant effect in the measured EEG signals, but it does not imply that these grid points are the true sources of the effect. MEG, either alone or in combination with EEG, could alleviate some of the ambiguity in EEG-only 2PN recordings [10].

The coupling of brain imaging with relevant behavioral measures in this study demonstrates that the 2PN approach can reveal critical aspects of social interaction that cannot be scrutinized in conventional single-subject settings. New analysis techniques still need to be developed for quantifying data from two-person recordings, such as capturing the time-variable properties of the interaction, as well as analyzing properties of the brain network comprising areas from both brains during the interaction.

Behavioral synchrony is critical for group performers, such as contemporary or ballet dancers, players in bands or chamber music ensembles, or soldiers in parade troops. However, synchrony alone is not enough to understand the basis of collaborative joint performance, where actions and interpretations of sensory information have to be shared across the dyad, but the partners have to take different, often counteracting, roles to reach the common goal.

Future research should also address the behavioral and neural basis of multiple hierarchical, simultaneously present time scales of social interaction, such as having a conversation with a friend while walking, with the quick steps synchronized, but the slower turn takings of the conversation anti-synchronized.

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Experimental, cultural, and neural evidence of deliberate prosociality

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A recent *PNAS* paper proposed that prosocial choice might be due to mistakes that disappear with learning. The authors' method for comparing preferences and mistakes might prove useful in other species. However, human evidence from various treatments, cultures, and the brain support the idea that humans are prosocial rather than mistaken.

In a recently published article, Burton-Chellew and West [1] suggest that apparently prosocial actions are just mistakes that humans have to learn to avoid. Their 'mistake hypothesis' (my term) is stated thus: '[. . .] participants enter the game uncertain of what the best decision is to maximize their earnings, and [. . .] they are largely indifferent to the welfare of others and operate with a myopic regard to their own welfare.' ([1], p. 218).

The mistake hypothesis is a possibility that is held dear in economics (where it is called 'confusion'). Respect for the mistake hypothesis in economics is a byproduct of the belief that people are fundamentally selfish, unless genetic kinship, legal or social punishment, or lost future gains from rupturing a repeated-game relationship create calculative

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prosociality. When early experiments that removed those conditions were conducted and substantial prosocial behavior was still observed, the mistake hypothesis gained traction.

Burton-Chellew and West's experiments find some support for the mistake hypothesis using public goods (PG) games. In these games, players can keep tokens, which have a private value of 1, or contribute them to their four-person group for a public value of 1.6 [of which they get one-fourth of the 1.6, a private per-capita return (MPRC) of 0.4]. Selfish players should not contribute anything.

As in hundreds of previous experiments, they find that players start giving approximately half their tokens, on average, with contributions falling over time: they give approximately 10-20% at the end (20 periods later) [2].

Other participants 'give' in an asocial 'black box' treatment, actually playing with others, but without being aware that they are interacting with others and knowing nothing about the payoff structure. Burton-Chellew and West find that the contribution pattern is similar in the PG and black box treatments in the MPCR = 0.4 treatment. This finding leads to their title conclusion that prosocial preferences do not 'necessarily' explain cooperation in PG games.

Their comparison between prosociality and mistakes in the black box treatment is forced, because theories of prosocial preference make no prediction in the black box treatment. How can evidence from an experiment that a theory does not apply to be considered as evidence against the theory? The answer, in their logic, is that the mistake hypothesis wins because it can be applied to both the PG and black box treatments – although only with the additionally maintained hypothesis that intelligent selfish subjects in the PG treatment 'are uncertain what the best decision is' (even though it is simple to figure out).

However, the totality of results in Burton-Chellew and West, including both the MPCR = 0.4 treatment and another MPCR = 1.6 treatment, are better explained by the prosociality hypothesis than the mistake hypothesis. The mistake hypothesis predicts similar patterns in both PG and black box treatments, controlling for MPCR, which is not what Burton-Chellew and West observed (because contributions are higher in PG than in black box when MPCR = 1.6). In addition, the prosociality hypothesis is supported by a host of other results, whereas the mistake hypothesis cannot gracefully account for any of them:

(i) There is a clear 'restart' effect, in which contributions jump up again when a multi-period PG experiment starts over, surprising the subjects [3,4]. The mistake-learning hypothesis predicts no restart.
(ii) In human experiments, prosocial action typically is sensitive to how much another person benefits. Indeed, Burton-Chellew and West's own data show such sensitivity: when MPCR = 1.6, giving in the PG and black box treatments is different (contrary to the mistake hypothesis). Furthermore, many other studies show that contribution rates depend on how much others benefit [4].
(iii) A plausible explanation for the coincident decline in giving in Burton-Chellew and West's PG treatment with MPRC = 0.4 is that subjects are conditionally cooperative at first, then stop giving when their contributions are not reciprocated. This explanation has direct support from experiments that elicit both giving choices and beliefs about whether others will give [5]. Those who give expect others will give too. Their contributions decline over time as they learn that others do not give.
(iv) Preplay communication among players about what they intend to do increases cooperation, even in one-shot stranger games. If people seek to avoid a mistake and are indifferent to welfare of others, talking about what to do should only help them realize that giving reduces their earnings, therefore reducing giving. However, talking increases cooperation, rather than reducing it [2].
(v) Prosociality varies across small-scale cultures in plausible ways that are not mistake-related. In these groups, literacy is low and confusion is more likely than in highly educated Western groups, which gives the null mistake hypothesis its best chance. However, public good production and market trading both enhance prosocial sharing [6].
(vi) If prosocial choices were mistakes, individuals would not be persistently prosocial across different games. Nonetheless, there is tentative evidence of such intra-subject differences [7].
(vii) Neural evidence indicates prosocial choices activate reward regions, as one would expect if they reflect preferences [8].
(viii) The mistake hypothesis was rejected in a very recent publication quite similar to Burton-Chellew and West's in design [9].

Ending on a constructive note, here is an experimental condition in which the social preference and mistake hypotheses make clearly different predictions:

Take the PG game and add costly punishment. After putting in 0–40 tokens, participants receive feedback about the contributions of other subjects. Then they can put in 1 token to subtract 3 tokens from one other group member (a 'punishment')... (This treatment is easy to do in both PG and in a black box treatment, where subjects can just choose to spend 1 token, but do not know the consequences for others.)

The predictions would be as follows: since punishment in the black box treatment costs tokens and only has a benefit if punished participants give more afterward, participants will typically not punish. However, costly punishment in PG games increases contributions [10]. Therefore, the contribution levels with punishment in subject pools like Burton-Chellew and West's will go up over time in PG games and will go down over time in the black box treatment. I am confident this result will occur and create new data the mistake hypothesis cannot account for.

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Article

Experimental, cultural, and neural evidence of deliberate prosociality

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Measuring pro-social preferences and the scientific method

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We thank Camerer for his spotlight on our recent paper [1]. However, his comments: (1) did not address the reason that our work was required; (2) did not provide an alternative explanation for our results; (3) misleadingly characterize our explanation; (4) provide no examples of data that can only be explained by pro-sociality, and (5) ignore data that cannot be explained by pro-sociality (the enhanced information treatment). More generally, his spotlight emphasizes the need for more rigorous scientific methodology in this area of research.

First, we pointed out that previous claims about pro-social preferences in humans were based on poor scientific method, including a lack of both a null hypothesis and experimental controls [1,2]. Without these, scientific claims cannot be made. Camerer does not dispute our claims on this point.

Second, we suggested a null hypothesis, the black box treatment, and a control (MPCR = 1.6), that would allow pro-social preferences to be more scientifically tested for [1]. Our results showed that: (a) humans cooperate to the same degree even when they do not know they are helping others (null model); (b) greater knowledge of helping others led to lower not higher cooperation; (c) the control treatment showed lower levels of cooperation than expected from self-interest (fewer than half the participants contributed fully even when it was in their own interest, and thus paid to harm others). Regarding these results, Camerer disputes (a), but provides no alternative null model, and ignores (b) and (c).

Third, Camerer distorts our explanation for our results by referring to it as the 'mistake hypothesis'. This is misleading, because it suggests that we claim that all our results are explained by mistakes. Instead, we just pointed out that all our results could be explained without the need to invoke pro-social preferences. The term 'mistakes' is also potentially a source of confusion as it can serve many definitions. A participant's failure to maximize their income in such games, which is after all the robust phenomenon much research aims to explain, may be the result of cognitive mistakes and/or evolutionary 'mistakes'. The former could arise from fully selfishly motivated players that misunderstand the game, whereas that latter can arise for many reasons, but primarily because we have not evolved to play economic games. Camerer asserts that mistakes and confusion are unlikely because "the best decision… is simple to figure out.", but whether this is true or not needs to be scientifically ascertained rather than merely asserted.

Fourth, the largest part of Camerer's spotlight was taken up by listing data that he argues is consistent with pro-social preferences, but not with what he terms the 'mistake hypothesis'. However, the examples he gives are easily explained by either 'mistakes' in the broad sense or pro-social preferences. Consequently, these data do not help distinguish between these hypotheses at all. For example: (i) a higher MPCR leads to a greater gain to self and social partners, and so greater cooperation would be expected from pro-social preferences, or a learning model, or merely a rule of thumb that proscribes help less when it costs you more; (ii) arguments about 'conditional cooperators' have also been based on experiments that lack controls and null hypotheses; (iii) pre-play communication brings in cues that aid cooperation in numerous ways, not just pro-social preferences; (iv) cultural variation is also predicted by both pro-social preferences and explanations that involve rules of thumb shaped by local experiences; (v) the cross cultural 'evidence' is primarily from data on the Ultimatum Game, which is a very poor test of pro-sociality; (vi) neural evidence provides no evidence to discern between the competing hypotheses.

Camerer's list of studies also emphasizes how the scientific method relies on not just appropriate controls and null models, but attempts to falsify hypotheses [3]. Listing a number of patterns consistent with one hypothesis has little scientific utility when they are also consistent with competing hypotheses. Hypotheses can only be distinguished between with implementation of rigorous scientific methods. In the specific case of human economic experiments, there are multiple explanations for why people may fail to maximize their earnings. Consequently, the scientific method requires that we use experiments to try to distinguish between these experiments, and not just assume that one preferred explanation is correct.

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